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## ORIGINAL ARTICLE

### Susceptibility of rubber trees to *Loranthaceae* in Gabon

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In Gabon, two major species of *Loranthaceae*, *Phragmanthera capitata* (Sprengel) Balle and *Globimetula braunii* (Engl.) Danser to a lesser extent, parasitize *Hevea brasiliensis* (Müll.) Arg. The behavior of different clones of rubber trees facing the *Loranthaceae* parasitism has been studied in the large industrial plantation of Mitzi and in three neighboring smallholding plantations. The clones PR 261, RRIM 600 and PB 260, although never totally resistant, are far less susceptible to *Loranthaceae* than the clones AVROS 2037, PB 217, PB 235 and GT 1. The parasite development kinetics was more rapid on the most susceptible clones. Phellem thickness, cortical parenchyma thickness and tannin cell density were independent of susceptibility. The number of tree ramifications was significantly different between the clones. Interestingly, on the least susceptible trees, being also the most ramified, the parasite showed the slowest development.

**Keywords:** rubber tree; *Loranthaceae*; *Phragmanthera capitata*; susceptibility; mistletoe; Gabon

#### Introduction

In Gabon, the cultivation of rubber tree, *Hevea brasiliensis* (Müll.) Arg., was first introduced during World War II to supply rubber for the Allied nations (Serier 1985), and then given up soon after the war. It was reintroduced in the 1980s to diversify the economy of the country, which was mainly depending on its oil reserves (Chambrier 1990).

The rubber tree, grown for its latex, has been introduced in various regions of the world where it is a target for specific parasitic plants belonging to the *Loranthaceae* family, e.g. *Taxillus chinensis* and *Dendrophthoe pentandra* in China (Zhiwei et al. 1995), and *Phragmanthera capitata* in most African plantations, namely in Cameroon (Sallé 1994; HE-VECAM 1995), Nigeria (Gill and Onybé 1990; Akinlabi and Aigbodion 2005) and Gabon (Guyot and Ntawanga 1998; Engone Obiang 2006; Engone Obiang and Sallé 2006).

The *Loranthaceae*, thoroughly studied by Balle and Hallé (1961) and Polhill and Wiens (1998), consist of small chlorophyllous epiphytic shrubs living as hemiparasites on branches of wild or cultivated trees. These hemiparasites look like clumps anchored in the wood of the host through a specialized organ, the haustorium, which establishes functional connections with the host vascular tissues. Through the haustorium, the parasite pumps in water, mineral salts and the organic matter required for its development from the host (Kuijt 1969; Sallé et al. 1998).

The infestation of rubber trees by *Loranthaceae* is one of the main phytosanitary problems encountered in Gabon, especially within the country's main plantation located in Mitzi where *Phragmanthera capitata* is by far the most common parasite (Guyot and Ntawanga 1998; Engone Obiang 2006; Engone Obiang and Sallé 2006).

Previous research carried out on *Viscaceae* showed a susceptibility gradient to parasitic epiphytes on hardwood trees. For example, studies concerning the associations of poplar/*Viscum album* (Frochot et al 1978) and oak/*Viscum album* (Grazi and Urech 1983) led to the identification of some resistant cultivars to the European mistletoe. Parameters involved in this resistance are now well documented, i.e. anatomical structures and phenolic compounds (Armilotta 1984; Sallé et al. 1984; Hariri 1989; Hariri et al. 1991, 1992; Sallé et al. 1993). Nevertheless, these studies did not take into account the effect of the morphology of the host's tree crown.

*Phragmanthera capitata* and *Globimetula braunii* are the major species of *Loranthaceae* among the nine species identified on rubber trees in Mitzi's zone (Engone Obiang 2006). *Phragmanthera capitata* is the most invasive as it parasitizes 95% of the rubber trees, whereas *G. braunii* attacks only 5% of the trees.

In this article, we put forward a methodology applying the anatomical and histochemical methods mentioned above but also involving the influence of the morphology of the host's ramification. The aim of this work is to establish a relationship between susceptibility to *Loranthaceae*, and either anatomical

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(phellem and cortical parenchyma thicknesses), or histochemical (tannin cell density) or morphological (the number of primary branches) characteristics.

## Materials and methods

### Study area and experimental design

Our data were mainly collected in the largest industrial rubber tree plantation of Mitzic and in three neighboring smallholding plantations named 1M2, M05 and M07.

The industrial plantation of Mitzic (lat. 0°50' N, long. 11°50' E, alt. 550 m) is divided into 14 sectors separated by swamps. Every sector consists of a variable number of plots. Generally, a plot is a surface comprising trees of a single clone, planted in the same year. However, AA01 and AA02 are clone trials, i.e. plots consisting of four replications obtained from one another by permuting six clones. Every clone of AA01 (AVROS 2037, GT 1, PB 217, PB 235, PR 261 and RRIM 600) contains 80 individuals, and every clone of AA02 (i.e. GGT 1, IRCA 109, IRCA 111, IRCA 130, RRIC 100 and RRIM 712), 108 individuals.

Whatever the type of plantation, trees are arranged in rows whose number varies according to the plot. However, distances between rows and between trees on a single row are constant, 7.5 m and 2.4 m, respectively.

### Estimation of the parasitism level

To estimate the parasitism level of the rubber tree clones, a survey was performed in various plots (5/12, 4/2, 3/1, 7/5, 1/0 3/9, AA01 and AA02) of the industrial plantation of Mitzic and nearby smallholding plantations 1M2, M05 and M07. The sample thus obtained comprised 15,739 trees; for each of them, the number of clumps and the names of the *Loranthaceae* species were recorded. For a given clone, the parasitism rate (Pr) is defined as follows:

$$\text{Pr} = \left[ \frac{\text{(number of parasitized trees)}}{\text{(total number of trees)}} \right] \times 100.$$

According to this measure of host susceptibility to the parasite, trees were distributed into three classes: non-parasitized (without visible clumps), moderately parasitized (with one to five clumps) and highly parasitized (with more than five clumps).

In the industrial plantation, the trees thus classed belonged to the six following clones: PB 217, GT 1, PB 235, AVROS 2037, PR 261 and RRIM 600. The smallholding plantation M07 comprises three clone types, PB 235, PB 260 and GT 1; whereas, the other smallholding plantations, 1M2 and M05, are just composed of one single clone type, GT 1.

First, a test for equality of proportions was performed to show whether susceptibility to *Loranthaceae* significantly differed from one clone to another. Then, a correspondence analysis (CA) was

carried out to visualize the relationships between clones and susceptibility to *Loranthaceae*.

### Artificial infestations

Artificial infestations were performed according to the protocol proposed by Frochot and Sallé (1980), to follow the germination of *P. capitata* seeds and the attachment on the host, as well as to study the development kinetics of *P. capitata* on different rubber tree clones. Mature seeds of *P. capitata* were laid on branches of clones of variable susceptibility like AVROS 2037, GT 1, RRIM 600 and PB 260. After being submitted to outdoor drying, the viscin around the seeds hardens and allows the attachment on the host branches.

By means of one way-ANOVA tests, we compared – between the six clones – the percentage of germination and attachment on the one hand, and the length of the first leaves of the parasite, four months after infestation, on the other hand. This measure gave an idea about the parasite growth rate.

### Morphometric, anatomical and histochemical study

For the morphometric study, the number of the ramifications of the trunk was established on seven clones: PB 217, PB 235, AVROS 2037, GT 1, PR 261, RRIM 600 and PB 260. The first six clones were in the AA01 clone trial and the last one in the farmer plantation M07. For each clone, 300 trees were measured.

For the statistical analysis, Friedman's test was used to estimate the role of the clone factor independently of the rank which each clone occupies in a row, using the formula:

$$\text{Fr} = \left[ \frac{12}{nk(k+1)} \times \sum_{j=1}^k (R^j)^2 \right] - 3n(k+1). \quad (1)$$

In this formula,  $n$  is the total number of clones in the AA01 clone trial,  $k$  the number of repetition and  $R^j$  the rank occupied by clones in the repetition.

A correspondence analysis enabled us to look for possible relationships between the clones and the number of branches, using Sturges' criterion for establishing the  $K$  intervals of the discretized of the number of branches. The number  $K$  depends on  $N$ , the number of branches, according to the formula:

$$K = 1 + \left\lceil 10 \frac{\log_{10} N}{3} \right\rceil. \quad (2)$$

The anatomical and histochemical studies were carried out on non-parasitized branch fragments of 22-year-old rubber trees belonging to the six clones, PB 217, AVROS 2037, GT 1, PR 261, RRIM 600 and PB 260, each clone containing three individuals. Bark samples were fixed with a Regaud solution, which precipitates phenolic compounds that turn then into a brownish color.

Thirty  $\mu\text{m}$  thick sections were performed using a frozen microtome Jung AG Heiberg type. For each individual, ten samples of about  $25\text{ mm}^2$  section were cut. Thin sections were mounted in glycerin.

To estimate the tannin cell density in the ten branch fragments of the three individuals belonging to each clone studied, 35 sectors of  $260\text{ }\mu\text{m}$  side length were delineated on a tracing paper. The number of tannin cells was estimated for each sector on the screen of a Reichert Visopan (Austria). A comparative study on the bark pertaining to the six rubber tree clones was performed to detect a possible anatomical variability in relation with susceptibility to *Loranthaceae*. Phellem and cortical parenchyma thicknesses were measured using a Reichert (Austria) micrometer objective for the ten sections observed.

Three one-way ANOVAs tested whether the susceptibility of the six clones differed significantly, each analysis being carried out for a given variable: phellem thickness, cortical parenchyma thickness or tannin cell density.

All the statistical analyses were performed by means of the R statistical processor (R Development Core Team 2005).

## Results

### *Infestation level by Loranthaceae in the industrial and smallholding plantations of Mitzić*

During our survey of the plantations studied, more than 15,000 trees scattered in the observed clones were studied and yielded the following information (Table 1): Parasitism rates varied between 19% and 91%, and differed significantly between the clones ( $F = 460$ ,  $p < 0.001$ ).

Parasitism level remained very high for AVROS 2037, PB 235 and GT 1 in all the plantations prospected so far. Remarkably, no rubber tree clone was totally devoid of parasites. In these plantations, there existed no rubber tree clone completely resistant to one or another form of *Loranthaceae*. At the opposite of clone trial AA01 characterized by a very high parasitism rate (76%, see Table 1), clone trial AA02 showed a much smaller one (26%). This discrepancy is easily explained; AA02 was subjected to a mechanical eradication of *Loranthaceae* in 1996, an event prior to which parasitism was rated low on young trees (3%).

The distribution of trees in three classes of susceptibility to the parasite (see *Materials and methods* section) was very useful for correspondence analyses (CA) to visualize the differences in the behavior of the clones facing the parasite. For the two types of plantation (the industrial and smallholding ones), correspondence analyses were carried out (Figures 1 and 2) and built up a good representation of the sets of clones and their corresponding susceptibility levels.

Table 1. Parasitism rate (%) on rubber trees in the clones and various plot types in Mitzić's industrial and smallholding plantations. The identification of every plot meets the denomination applied by the managers of Mitzić's industrial and smallholding plantations. Every plot comprises only one clone type except for AA01 and AA02 (polyclonal trials).

Clones	Plot identification	Number of observed individuals	Parasitism rate (%)
AVROS 2037	4/2	1606	91
PB 235	3/1	1733	84
GT 1	1/0	1091	82
PR 261	5/12	3348	50
PB 260	7/5	736	19
RRIM 600	3/9	1009	37
GT 1	AA01	311	97
PB 235	AA01	303	80
PB 217	AA01	251	94
PB 261	AA01	310	77
AVROS 2037	AA01	303	89
RRIM 600	AA01	315	63
IRCA 130	AA02	303	35
RRIM 712	AA02	407	23
RRIC 100	AA02	405	6
IRCA 111	AA02	412	33
IRCA 109	AA02	395	71
GT 1	AA02	411	41
GT 1	PV 1M2	466	86
GT 1	PV M05	337	91
GT 1	PV M07	205	96
PB 260	PV M07	982	30

SP, smallholding plantations.

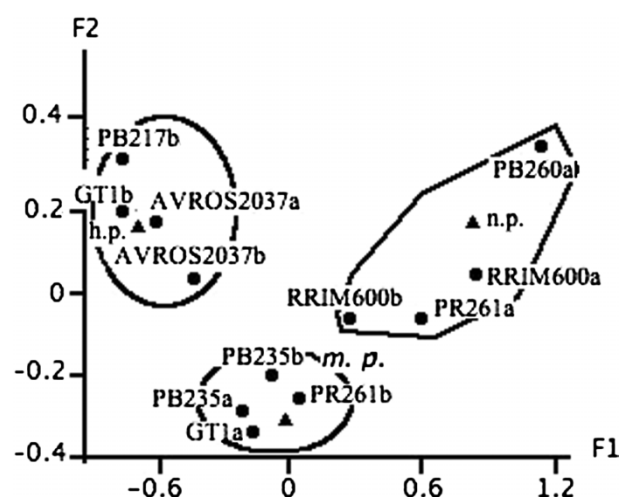


Figure 1. Correspondence analysis visualizing the responses of rubber tree clones to the *Loranthaceae* in the plots from Mitzić's industrial plantation. The indices a and b represent, respectively, clones planted in the plots not belonging to the clones trials, and clones planted in clone trial AA01. Triangles represent the susceptibility levels and circles, the clones. Respective inertia rates of the factorial axes F1 and F2: 87.2% and 12.8%. n.p., not parasitized; m.p., moderately parasitized; h.p., highly parasitized.

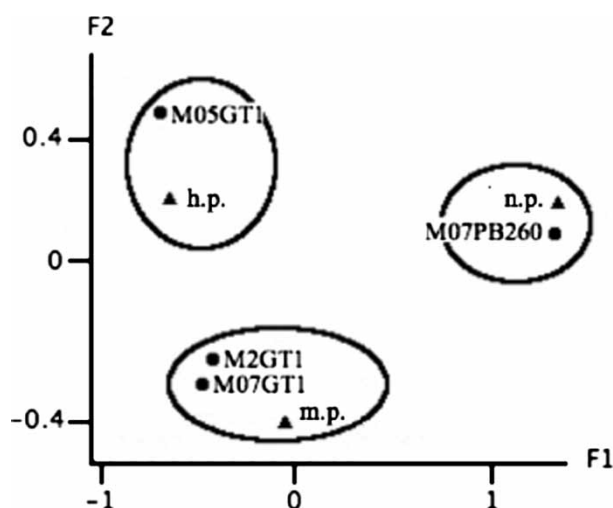


Figure 2. Correspondence analysis visualizing the responses of the clones to the *Loranthaceae* in the smallholding plantations. The triangles represent the susceptibility levels; and circles, the clones. Respective inertia rates of the factorial axes F1 and F2: 90.8% and 9.2%. n.p., not parasitized; m.p., moderately parasitized; h.p., highly parasitized.

It is noteworthy to specify that in the industrial plantation, clones planted in the monoclonal plots were labeled 'a', while the others belonging to the AA01 clone trials were labelled 'b'. One of the CAs (Figure 1) showed that the clones RRIM 600a, PB 260a, PR 261a and RRIM 600b were lowly parasitized (meaning in this case that most of the trees from the clone are healthy), whereas PB235b, PB 235a, PR 261b and GT 1a were moderately parasitized, and AVROS 2037a, AVROS 2037b, PB 217b and GT 1b were highly parasitized.

The same statistical analysis performed in the smallholding plantations (Figure 2), showed that the clone PB 260 was lowly parasitized, whereas GT 1 was moderately or highly parasitized.

The two analyses yielded very consistent results. In both cases, PB 260 was lowly parasitized and GT 1, moderately or highly parasitized. Thus, a susceptibility gradient could already be put forward, ranging from the most susceptible to the least susceptible: PB 217, AVROS 2037, GT 1, PB 235, PR 261, RRIM 600 and PB 260.

#### Development kinetics of *Loranthaceae* on several rubber tree clones

Table 2 shows the development kinetics of *Loranthaceae* after artificial infestations performed on four rubber tree clones listed according to their decreasing susceptibility level (AVROS 2037, GT 1, RRIM 600 and PB 260). For all the clones, the percentage of germination was high, exceeding 75%, whereas the percentages of attachment on host branches were much lower, close to 30%. No significant difference was observed between the clones concerning the success of germination or attachment (the F values

Table 2. Results from artificial infestations with seeds of *P. capitata*. Germination and attachment rates (% in brackets) are given by the following formulae:

$$Gr = \frac{\text{number of germinated seeds}}{\text{number of applied seeds}} \times 100 \text{ and}$$

$$Ar = \frac{\text{number of plantlets}}{\text{number of germinated seeds}} \times 100.$$

	Number of seeds applied on branches	Number of germinated seeds (dfs: 3 and 710)	Number of plantlets (dfs: 3 and 208)
PB 260	209	170 (81)	53 (31)
RRIM 600	229	190 (83)	60 (32)
GT 1	220	180 (82)	52 (28)
AVROS 2037	229	174 (76)	47 (27)
Total	887	714	212

being, respectively,  $F = 1.4$  (dfs = 3 and 710),  $p > 0.05$  and  $F = 0.4$  (dfs = 3 and 208,  $p > 0.05$ ). Hence, no significant clone effect was detectable on germination or attachment success.

However, when the development of the 212 plantlets (see Figure 2) was followed during four months (Figure 3 and Table 3), a significant 'clone' effect could be shown regarding the length of the first leaves ( $F = 54.9$ ;  $df = 3$  and 208;  $p < 0.05$ ). The plantlets developing on AVROS 2037 and GT 1 had longer leaves, respectively 38.8 and 22.1 mm, than those growing on PB 260 and RRIM 600, respectively 16.1 and 17.0 mm.

The Neuman-Keuls test (Table 3) identified three different groups of plantlets, which were assigned 'A', 'B' and 'C', the alphabetic order of these chosen letters being in parallel with the increasing order of the length of their first leaves, in turn in parallel with

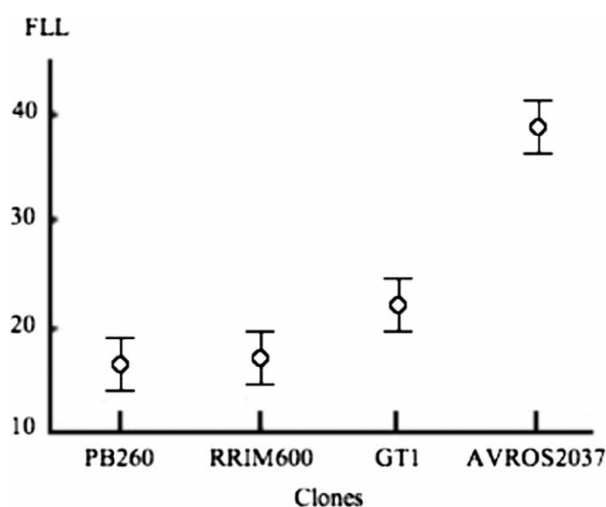


Figure 3. Development of the *Phragmanthera capitata* plantlets on branches belonging to four rubber tree clones. The circles represent the length in mm of the first leaves of the plantlets; and the vertical bars, the 95% confidence intervals of the mean values. Abscissae = the different clones, ordinates = First leaves lengths (FLL).

Table 3. Clone assignment to groups (Neuman-Keuls test). Each clone, characterized by a mean leaf length value, is assigned to one and only one among three labels, A, B or C. Each assignment corresponds to the clone's membership to a single specific interval whose leaf mean length varies between two bounds; the three intervals are adjacent, and their reunion equal to the interval of all the values taken on by the clones. The bounds are fixed by a criterion of the test.

Clones	Leaf mean length (mm)	Groups
PB 260	16.18	A
RRIM 600	17.03	A
GT 1	22.17	B
AVROS 2037	38.85	C

the increasing order of development speediness. Hence, we inferred that in the least susceptible clones RRIM 600 and PB 260 (the members of the A group), the development of the plantlets was slow, in comparison to the plantlet behavior in the other clones. Interestingly, the leaf development was more rapid in a moderately susceptible clone, GT 1 (member of the B group) and still faster in the most susceptible clone like AVROS 2037 (member of the C group).

This kinetic approach suggests that the more the rubber tree is susceptible to *P. capitata*, the more rapid the development of the parasite tends to be.

#### Ramification effect on the susceptibility of the different clones

This morphometric study treats the effect of the ramification of the first order on the susceptibility of six clones – AVROS 2037, GT 1, PB 235, PB 217, PR 261 and RRIM 600 – from the AA01 clone trial. The numbers of branches of the relevant ramifications were estimated on the clones just mentioned above and ranged from 4.6 to 16.3 (Table 4). Individuals of RRIM 600 and PR 261 were always much more ramified than the others. The Friedman's test confirmed these observations and indicated the existence of a 'ramification' effect on the susceptibility of the clones ( $Fr = 8.4$ ,  $p < 0.05$ ).

Table 4. Mean number of branches per clone in the various plots. Clones RRIM 600 and PR 261 are lowly susceptible to the *Loranthaceae*, and clones AVROS 2037, PB 217 and GT 1 highly susceptible.

	Plot 1	Plot 2	Plot 3	Plot 4
GT 1	12.0	10.4	9.9	9.3
RRIM 600	16.1	13.3	15.6	14.4
PB 217	11.0	7.7	8.1	11.6
PB 235	8.9	7.6	7.2	11.7
AVROS 2037	8.1	6.5	4.6	6.5
PR 261	16.3	11.7	11.4	13.3

To carry out correspondence analysis on clones and ramification, the numbers of the observed branches of the first order were distributed in different classes according to the criterion of Sturges. For this study, a seventh clone was added, PB 260, because of its very low level of parasitism (see Figure 2) and its absence in the AA01 clone trial. So far, four classes of ramification levels were determined: [0–5], [6–11], [12–17] and [18–60].

The analysis showed that trees belonging to the most susceptible clones like AVROS 2037, PB 235, PB 217 and GT 1 (Figure 4), displayed very little ramification since they belonged to the [0–5] and the [6–11] classes. On the contrary, most individuals from the least susceptible clones like RRIM 600, PR 261 and PB 260, corresponded to the intervals including the highest ramification values [12–17] and [18–60]. Therefore, a relationship could be established between susceptibility and ramification, high ramification corresponding to a low parasitism rate.

#### Location and density of the tannin cells

The location of tannin cells was studied on longitudinal radial sections of branches pertaining to six rubber tree clones. These compounds are located in the vacuole of the cortical parenchyma cells. Observations showed no differences in the density of tannin cells according to the clones.

A one-way ANOVA (Table 5) was applied to each of the three following variables, i.e. phellem thickness, cortical parenchyma thickness and tannin cell density. According to the data set, no significant difference could be shown between each of the variables just mentioned and the clones. This statistical analysis is illustrated by the empirical diagram where a number of overlapping 95% confidence intervals has been displayed (Figure 5).

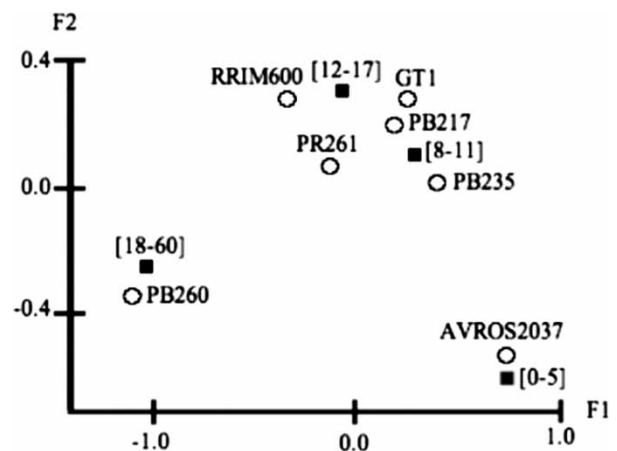


Figure 4. Correspondence analysis visualizing the clone effect on the number of branches. The filled squares represent the number of branches (intervals in square brackets next to the symbols); and circles, the clones. Respective inertia rates of the factorial axes F1 and F2: 77.4% and 21.4%.

Table 5. One-way ANOVAs on the three variables.

	PB 260	RRIM 600	PR 261	GT 1	AVROS 2037	PB 217	Statistics	
							F	p value
MPT ( $\mu\text{m}$ )	106	146	136	126	126	136	2,4	0.11
MCPT ( $\mu\text{m}$ )	233	276	270	303	230	290	2,02	0.146
MTDXD	38	37	34	37	38	43	1.03	0.44

MPT, mean phellem thickness; MCPT, mean cortical parenchyma thickness; MTCD, mean tannin cell density; F, Fisher statistics, differences being significant when  $p < 5\%$ .

## Discussion

Data collected in the area of Mitzi, from the industrial and smallholding plantations of rubber trees, showed that *Loranthaceae* were very common and that among them *Phragmanthera capitata* was, by far, the most widespread (95%). The level of parasitism by *P. capitata*, estimated on more than 15,000 rubber trees, widely varied according to the clone. The clones AVROS 2037, PB 217, PB 235 and GT 1 were highly parasitized whereas PR 261, RRIM 600 and PB 260 were less attacked. This gradient of susceptibility is fully consistent with the previous observations of Guyot and Ntawanga (1998) who found, in experimental plots of the C.A.T.H. (Centre d'Appui Technique à l'Hévéaculture), that whatever the type of plantation (industrial or smallholding), RRIM 600 was always less susceptible than PB 217 and GT 1. In our study, another clone, PB 260, turned out to be slightly susceptible to *P. capitata*.

It is noteworthy that rubber trees never displayed a complete resistance to mistletoe in contrast with some cultivars of poplars, such as Blanc de Garonne and Vereecken, totally resistant to *Viscum album* (Frochot et al. 1978; Armillotta 1984; Hariri 1989;

Hariri et al. 1992), which never hosted mistletoe in natural conditions or after artificial infestations.

In the associations poplar/*V. album* and oak/*V. album*, several parameters involved in resistance were well established (Hariri 1989; Hariri et al. 1991): Anatomical features (phellem thickness, cortical parenchyma thickness), or biochemical characteristics (tannin-rich cell density). Moreover, it was shown on poplars that a positive correlation existed between these parameters and the behavior of mistletoe (Hariri 1989; Hariri et al. 1991, 1992): the higher the values of these three variables, the more resistant the cultivar was. As far as rubber tree is concerned, no relation between these parameters and the susceptibility to *Loranthaceae* could be observed. This is consistent with previous data showing the absence of a true resistance in rubber trees (Guyot and Ntawanga 1998; Engone Obiang 2006).

On the other hand, the ramification level is significantly correlated to the susceptibility to *Loranthaceae*. We established statistically that the most susceptible clones like AVROS 2037, PB 217, PB 235 and GT 1 showed few ramifications, whereas the least susceptible like PR 261, RRIM 600 and PB 260 were the most branched. These results are in agreement with those of Combes and Du Plessix (1974) who observed that RRIM 600 had the highest number of lateral buds, well known to generate branches. In addition, results concerning the development kinetics of *P. capitata* on different clones also support this idea. Plantlets developed much more rapidly on susceptible clones, like AVROS 2037. Accessibility of light to parasites could easily account for these observations. As it is well known that light is crucial for mistletoe development (Lamont and Perry 1977), there is evidence that rubber trees with few branches, therefore with sparse foliage, allow a better access of sunlight to parasites. We must notice that the high incidence of *Loranthaceae* in Mitzi plantations is the consequence of *Colletotrichum* leaf disease: The canopy of rubber trees has been strongly affected for many years with a harmful incidence on the foliage density.

During artificial infestations performed on different rubber tree clones, it was noted that percentages of germination and attachment on the host were not significantly different from one clone to another. These results match well with our knowl-

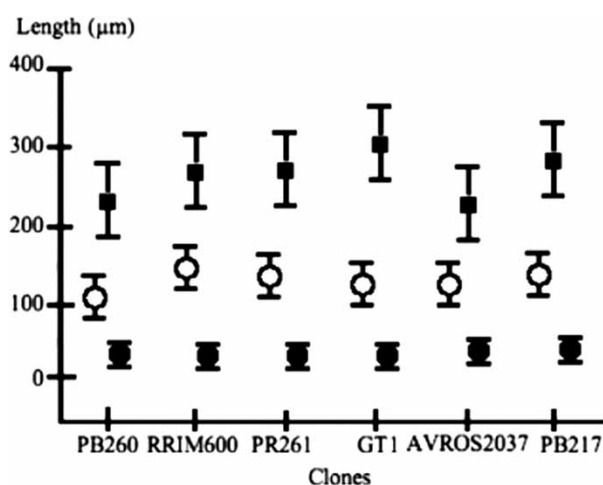


Figure 5. Simultaneous representation of three variables. The filled squares represent the mean parenchyma thickness ( $\mu\text{m}$ ); the empty circles, phellem thickness ( $\mu\text{m}$ ); the filled square, cell density per  $260 \times 260 \mu\text{m}$  sector. Vertical bars represent the 95% confidence intervals of the mean lengths per clone.

edge of the biological cycle of *Loranthaceae* and *Viscaceae*: they germinate whatever the substratum (Sallé 1975; Clay et al. 1985). However, further development of plantlets requires a live and compatible host. Some of the reasons for the resistance lie in the development during the early growth of the haustorium (Hariri et al. 1990, 1991; Sallé et al. 1993). In all poplar cultivars, it was shown that the onset of development of the primary haustorium provoked a breakdown of phellem and a division of the phellogen, the inner part giving rise to an inner phellem which enclosed the young primary haustorium. The periaustorial zone formed at that stage contained polyphenolic substances. On the behavior of this mechanico-chemical barrier depends the success or the failure of the association. In very susceptible cultivars like Fritzky Pauley, the young primary haustorium passed rapidly through the inner phellem and the host secreted few polyphenols. On the contrary, in resistant cultivars such as Blanc de Garonne and Vereecken, the host reacted more intensively against the parasitic attack: The inner phellem was never broken and the synthesis of polyphenols was enhanced. In these conditions, the parasite never reached live host tissues and consequently the plantlet died.

In rubber trees, even in the least susceptible clones such as PB 260, histological sections performed on four-month-old plantlets (Engone Obiang 2006), showed that the young primary haustorium always reached the host live tissues, so that the plantlet could keep on growing.

## Conclusion

Our study carried out on several rubber tree clones leads to four important conclusions:

- (1) In the association *Hevea brasiliensis*/*Phragmanthera capitata*, total resistance to *Loranthaceae* does not exist. A gradient of susceptibility can be proposed ranging from highly susceptible clones (AVROS 2037, GT 1, PB 217 and PB 235) to lowly susceptible ones (PR 261, RRIM 600 and PB 260).
- (2) The development of mistletoe is significantly and positively correlated to the susceptibility of the clone: the slower the parasite development, the less susceptible the clone is. However, the haustorium develops in all clones.
- (3) No positive correlation can be established significantly between susceptibility and the anatomical or biochemical characteristics studied here.
- (4) Susceptibility of rubber trees to *Loranthaceae* is negatively correlated to host ramification: the more ramified the rubber tree is, the slower the parasite develops and the less susceptible the clone is.

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